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Formation of Oleoresin and Lignans in Sapwood of White Spruce in Response to Wounding

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ABSTRACT

Sapwood of white spruce (*Picea glauca*) was wounded in the spring with an increment borer. Tissue adjacent to the wound, collected 4-9 months after injury, was more decay resistant than uninjured tissue when exposed to *Poria monticola* or *Coriolus versicolor*. No significant quantitative or qualitative differences in lignans were observed between injured and uninjured sapwood. Injured sapwood contained 30% heptane solubles, compared to approximately 2% for uninjured sapwood or heartwood. This heptane fraction contained almost entirely resin acids. Impregnation of decay-susceptible wood of cottonwood (*Populus deltoides*) with dehydroabietic acid, or with a mixture of resin acids, resulted in a similar increase in decay resistance.

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Certain stimuli (aging, mechanical injury, attack by a pathogen) cause cytological and chemical changes in the living cells of sapwood of both conifers and woody angiosperms. One phenomemon commonly observed is the formation of compounds such as lignans, stilbenes, resin acids, tannins, etc. Some of the compounds formed in response to injury or pathogenic attack have antimicrobial properties, and hence may have a role in limiting subsequent invasion by pathogenic organisms.

Reaction zone tissue, which develops between sapwood and the brownish central core of wood decayed by *Fomes annosus* in Norway spruce (*Picea abies*), was found to be significantly more resistant to decay than sound heartwood or sapwood (16). A high hydroxymataresinol concentration in association with the alkalinity of the reaction zone contributes to the resistance of this tissue (17).

The objective of our study was to determine if mechanical injury to the sapwood of white spruce (*Picea glauca*[Moench] Voss) produced decay resistant tissue and, if so, to identify the factor(s) responsible for the increase in decay resistance.

MATERIALS AND METHODS.—The white spruce were located at W.K. Kellogg Forest, Augusta, Michigan, and occupied an intermediate crown position in a closed pure stand. They were 13 cm in diameter 1.4 m above ground and contained 8-12 and 14-16 growth rings of sapwood and heartwood, respectively. Trees were injured with an increment borer during April, 1970, and were harvested in August, 1970 (four trees) or January, 1971 (two trees). Twelve holes in three rows (four holes/row) or 20 holes in four rows (five holes/row) were bored into each tree approximately 1.5 m above the ground. Depth of the borer holes was approximately 3.0 - 3.5 cm and the holes did not penetrate into the heartwood. Horizontal and vertical distance between holes was 6-9 cm. After harvest, a section of the trunk was removed with the rows of borer holes located in the middle. Ends of the logs and borer holes were covered with aluminum foil to reduce desiccation. Within 4 hours after harvest, logs were cut into cross-sections 1-2 cm thick and stored at −5 C for later study.

Decay tests.—Decay tests employing the agar-block method (13) were conducted on the various tissues (three-to-four replicates per tissue per tree) to compare their relative susceptibility to decay by the white-rot fungus, *Coriolus versicolor* (L.) Quel. (Madison 697) previously known as *Polyporus versicolor* L. ex Fr., and the brown-rot fungus *Poria monticola* Murr. (Madison 698). Sapwood, heartwood, and discolored wood (tissue immediately above or below the borer hole) were cut into blocks approximately 1.5 cm (radial) and 0.8 cm (tangential and vertical). Initial dry weight was determined after blocks were conditioned for 14 days at 40 C. Blocks were sterilized with steam for 5 minutes at 90-100 C, and placed aseptically on a 4-mm diameter glass rod on the surface of the agar in decay chambers [226 ml (8-oz) French square glass bottles] which had been inoculated 14 days previously with a decay organism. The blocks were incubated for 6 weeks at 26 C, removed from the chambers, cleaned of fungal growth, and conditioned for 14 days at 40 C to determine final dry weight. Weight loss was expressed as a percentage of the initial oven-dry weight, and an analysis of variance was calculated for these data.

Defect-free blocks of cottonwood (*Populus deltoides* Bartr.) weighing 0.7 - 1.2 g and with dimensions 1.5 cm (radial), 1.0 cm (tangential), and 0.9 - 1.2 cm (vertical) were trimmed of loose wood. Initial dry weight was determined after blocks were conditioned for 14 days at 40 C. Blocks were placed under vacuum for 15 minutes and then infiltrated with the test solution for 15 minutes while still evacuated. Blocks were left in the test solution at atmospheric pressure for an additional 15 minutes (1). The blocks were impregnated with either dehydroabietic acid or a mixture of dehydroabietic and abietic acids dissolved in either acetone or hexane. Analyses by gas-liquid chromatography (GLC) showed that the dehydroabietic acid preparation was about 80% dehydroabietic acid, and the mixture contained approximately 35% each of abietic and dehydroabietic acids; the remainder of each sample being other resin acids and oxidized materials. The blocks were steam-sterilized at 99 C for 15-30 minutes and placed aseptically

into decay chambers inoculated with either *C. versicolor* or *P. monticola*. After 4 weeks at 27 C, the mycelium was brushed off the blocks which were dried for 48 hours at 95 C, and the weight loss determined. Blocks which were impregnated with solutions, but not inoculated were dried and weighed to determine uptake of extract.

Chemical analysis.—Samples of sapwood, heartwood, and discolored wood were cut from the two white spruce harvested in January, 1971 (designated A and B), allowed to air-dry for 72 hours, and ground in a Wiley mill to pass through a 2-mm (mesh-size) screen. The pH was measured by placing 4 g of each tissue into 100 ml of distilled water, soaking for 24 hours, and then determining (with a glass electrode) the pH of the cold-water extract.

A sample of each tissue was extracted for 6 hours in a Soxhlet apparatus with N-heptane followed by a 6-hour extraction with methanol. The percentage of each sample which was soluble in the two solvents was determined. Preliminary analysis of the methanol extract was accomplished by thin-layer (TLC) and paper chromatography (PC). TLC plates (Kieselgel GF 254 with a thickness of 0.25 mm) were developed in toluene:ethyl acetate:formic acid (5:4:1, v/v) or chloroform: ethyl acetate (7:4, v/v). Solvents used in PC were either 6% acetic acid or *n*-butanol:acetic acid:water (BAW) (6:1:2, v/v) in one dimension or BAW followed by 6% acetic acid in the second dimension. Authentic samples of matairesinol, hydroxymatairesinol, pinoresinol, and conidendrin were cochromatographed with the methanol extracts. Measured R_f values for lignans using these systems have previously been reported (12). Spots on chromatograms were detected under short-wave ultraviolet light or with diazotized sulfanilic acid (dSA) followed by 20% sodium carbonate. Diagnostic colors (hydroxymatairesinol, orange; matairesinol, rose; pinoresinol, blood red; and conidendrin, purple) resulted when the various authentic lignans reacted with dSA, thus enabling compounds with similar R_f values to be easily identified.

Estimates of the amounts of lignans present in each tissue were made by GLC using a Varian 2100 gas chromatograph with flame ionization detectors. A glass column 2 m long and 3-mm inside diameter packed with 3.6% Apiezon L on 177-149 μm (80- to 100-mesh) DMCS Chromosorb W was used. The carrier gas (nitrogen) flow rate was 50 ml/minute, while hydrogen and air flow rates were 35 ml/minute and 350 ml/minute, respectively. Detector and injection temperatures were 250 C, and initial oven temperature (200 C) was increased 1 C/minute to a final temperature of 240 C.

Seventy μliters of hexamethyldisilazane:trimethylchlorosilane:pyridine (2:1:10, v/v) and 30 μliters of *N,O-bis* trimethylsilylacetamide were successively added to a known amount (approximately 1 mg) of the vacuum-dried methanol extract. This mixture was briefly heated and after 15 minutes 5 μliters were injected into the chromatograph. Known amounts of matairesinol, liovil, and conidendrin were silylated in a similar fashion for calibration purposes. Previous work (12, 17) had shown that calibration curves for these lignans showed a linear response over the range of concentration that lignans were detected in wood. Authentic hydroxymatairesinol and pinoresinol were also used to establish their relative retention times (RRT). The five silylated authentic lignans were used as markers, both alone and in combination with the various silylated methanol extracts. RRT for the silylated lignans were: hydroxymatairesinol 1.00; liovil 0.80; matairesinol 1.13; conidendrin 1.28; and pinoresinol 1.68. Authentic lignans and extracts were also chromotographed under previously reported conditions

TABLE 1. Weight loss of blocks of sapwood, heartwood, and injured sapwood of white spruce exposed to *Coriolus versicolor* or to *Poria monticola* for 6 weeks at 26 C

Tissue	Weight loss (% dry weight)[1]	
	C. versicolor	*P. monticola*
Uninjured sapwood	13.9 a	42.3 a
Heartwood	14.7 a	45.8 a
Injured sapwood	2.9 b	25.5 b

Each mean is the average of five blocks of uninjured sapwood and heartwood or three blocks of injured sapwood from each of six trees; means in each column not followed by the same letter are significantly different $P = 0.01$.

TABLE 2. Amount (% of oven-dry wt.) of hydroxymatairesinol, liovil, and conidendrin in the uninjured sapwood (SW), heartwood (HW), and injured sapwood (ISW) of white spruce

	Tree A			Tree B		
	SW	HW	ISW	SW	HW	ISW
Hydroxy-matairesinol	0.10[a] ±	0.04	0.04	0.13	0.08	0.12
Liovil	0.02	0.02	0.01[b]	0.03	0.03	0.03[b]
Conidendrin	0.01	0.02	0.01	trace	0.02	0.03

[a] Average concentration of two-to-four determinations.
[b] Amount of liovil in ISW was difficult to measure accurately because of other compounds with similar retention times.

TABLE 3. Heptane and methanol-soluble materials (% of oven-dry wt) in white spruce wood

Tree and tissue	Heptane soluble (%)	Methanol soluble (%)
Tree A		
Uninjured sapwood	2.0	3.6
Heartwood	1.2	1.2
Injured sapwood	29.3	6.2[a]
Tree B		
Uninjured sapwood	2.4	3.4
Heartwood	1.7	1.4
Injured sapwood	34.0	10.0[a]

[a]Much of this extract was composed of terpenoids which were incompletely removed by petroleum extraction.

(12, 17) for comparative purposes. Two or more analyses were made of each extract.

The ultraviolet spectrum of the heptane solubles indicated a mixture of resin acids. Additional qualitative identification was by GLC, using previously described techniques (8, 9). A small sample of the heptane solubles from each wood type from trees A and B were methylated with ethereal diazomethane. The resin acid methyl esters were then injected into a Varian 2100 chromatograph on 2-m(long) × 3-mm (inside diameter) glass columns packed with 6% diethylene-glycol succinate on 177-149 μm particle size (80- to 100-mesh) Chromosorb W treated with dimethylchlorosilane. The nitrogen carrier gas flow rate was 50 ml/minute, while hydrogen and air-flow rates were 25 ml/minute and 275 ml/minute, respectively. Oven temperature was 180 C.

RESULTS.—At the time of harvest, the borer wounds were found to be plugged with an amorphous pale-pink to yellowish-white, sticky material. The wood next to the borer hole was infiltrated with a similar material for 3-5 mm tangentially and for 12-15 mm vertically.

Injured discolored sapwood was more resistant to decay than was uninjured sapwood or heartwood (Table 1). No differences in rates of decay were detected between the trees harvested in August (4 months after injury) and those harvested in January (9 months after injury). These results are very similar to those reported by Shain (16) where the reaction zone produced in the sapwood of *Picea abies* in response to fungal invasion was more resistant to decay by *Fomes annosus* than either sapwood or heartwood. However, in contrast to the results of Shain (16), the pH of the injured sapwood (5.0) was lower than that found for the uninjured sapwood (6.0) or for the heartwood (6.0).

When the methanol extracts were chromatogramed on Whatman No. 2 paper, a compound which reacted with dSA to give an orange spot at R_f 0.90 (BAW) and R_f 0.72 (6% acetic acid) was detected in all tissues. Authentic hydroxymatairesinol reacted in a similar manner. This compound and authentic hydroxymatairesinol ran at the same rate on TLC with both solvent systems. Some tissues, particularly the injured sapwood from tree B, contained a compound which reacted with dSA to give a purple spot at R_f values of 0.79 (BAW) and 0.0 (6% acetic acid). The R_f values and detection of this compound (conidendrin) were greatly influenced by the amount of resin in the sample; it could not be detected consistently in the uninjured sapwood and heartwood extractives. Neither pinoresinol nor matairesinol could be detected using either PC or TLC.

Analysis (GLC) of the methanol extracts from all three tissues showed compounds with the same RRT as authentic trimethylsilyl derivatives of liovil, hydroxymatairesinol, conidendrin, and trace amounts of pinoresinol. Matairesinol was not present in detectable amounts. There were no significant changes in either composition or amounts of lignans in the discolored sapwood zone compared with sapwood or heartwood (Table 2).

Injured sapwood contained considerably more heptane solubles (oleorisin) than did either the uninjured sapwood or heartwood (Table 3). Chromatographic analyses (GLC) revealed that the heptane solubles from injured sapwood were primarily the resin acids dehydroabietic, levopimaric-palustric, isopimaric, sandaracopimaric, abietic, pimaric, and neoabietic, listed in order of relative concentration. The heptane solubles from the sapwood and heartwood contained the same resin acids in the same relative order of concentration except that the peak represented by levopimaric-palustric acids was absent. These two compounds have the same RRT, and no attempt was made to characterize the combined peak.

Since neither alkaline pH nor a high hydroxymatairesinol content suggested (17) as responsible for the decay resistance of reaction-zone tissue in Norway spruce to *Fomes annosus*, occurred in injured sapwood, the high level of resin acids in this tissue was examined for their contribution to decay resistance. When cottonwood blocks were impregnated with an acetone-dehydroabietic acid solution, (38:100, w/w), there was 50% and 90% less weight loss caused by *Poria monticola* or *Coriolus versicolor*, respectively, than occurred in blocks impregnated with acetone alone (Table 4). Impregnation with a resin-acid mixture resulted in a similar, but smaller, increase in decay resistance. The use of heptane as a solvent for impregnating resin acids, resulted in a similar pattern of increased decay resistance to those shown in Table 4, although of somewhat lesser magnitude.

DISCUSSION.—Woody tissues adjacent to increment-borer wounds in *Picea glauca* had an acid pH, normal lignan concentrations, high resin-acid contents, and increased resistance to decay by *Poria monticola* and *Coriolus versicolor*. The acidic pH of the injured discolored sapwood tissue was in the range known to be favorable to the growth of decay fungi; hence, pH was not a significant cause of increased decay resistance. Shain and Hillis (17) found an alkaline pH in the reaction zone of *Picea abies* under attack by *Fomes annosus*. These differences in pH may reflect a different response to mechanical wounding, and to *F. annosus* attack.

Hydroxymatairesinol contents of sapwood, injured sapwood, and heartwood were similar (Table 2), whereas injured sapwood was much more resistant to decay by either fungus than was normal sapwood or heartwood

(Table 1). Therefore hydroxymatairesinol apparently was not important in the increased resistance of injured sapwood to decay by *P. monticola* or *C. versicolor*. The concentrations of lignans found in *P. glauca* heartwood agree closely with the values reported for *P. abies* heartwood (4). The amounts of lignans in the sapwood were similar to figures reported for the sapwood of *Tsuga heterophylla*, in which hydroxymatairesinol (0.255%) was found in a ratio of about 5:1 to that of conidendrin (0.05%), only a trace of pinoresinol (0.009%), and no matairesinol was found (6). However, Shain and Hillis (17) reported that neither hydroxymatairesinol nor conidendrin was present in detectable quantities in the sapwood of *P. abies*, but liovil was present in amounts similar to those found in *P. glauca*. While there was considerable variation between tissues of the two trees examined, the irregular distribution of lignans in *T. heterophylla* suggests that wide variations are to be expected unless large numbers of samples are examined (12).

Weinges (20) reported quantitative and qualitative changes (increases in pinoresinols and isolariciresinols) after mechanical injury to the cambial zone of *P. abies*. However, Shain and Hillis (17) found that the major response of the inner sapwood to *F. annosus* was a 15-fold increase in the concentration of hydroxymatairesinol in a narrow band around the affected tissue. In the present study, neither quantitative nor qualitative changes in lignan concentrations were observed. This may have resulted from the method of sampling, because Shain and Hillis (17) indicate that the increase in hydroxymatairesinol might not be detected unless very small serial samples taken through the reaction zone are examined. Parasite damage and mechanically inflicted injury often initiate the same response in plants, even though the triggering agents may not be the same (11). However, the differences in the results from studies by Weinges (20), Shain and Hillis (17), and our work suggests that lignan synthesis is a very specific response that varies with the stimulus. The irregular distribution of lignans in *T. heterophylla* supports this hypothesis (12). Matairesinol was found only in frost seams (12); such tissues contained very high concentrations of pure lignans. In other areas of the frost-injured tissue there were patches of either conidendrin (floccosoids) or hydroxymatairesinol.

The most probable cause for the observed increase in decay resistance is the high resin-acid content of injured sapwood (Tables 1 and 4). Injured sapwood, which is resin-soaked, decayed at about the same rate (Table 1) as did cottonwood blocks impregnated with 38% resin acids (Table 4). In both instances, decay caused by *C. versicolor* was reduced more than was decay caused by *P. monticola*.

Oleoresin (a solution of resin acids in a volatile oil) frequently accumulates at wounds or sites of infection in various coniferous species. These substances might account for resistance of the wood to bacterial, fungal, or insect invasion. Data on the effectiveness of these substances in preventing or reducing invasion by microorganisms are conflicting. Resin acids at 40 μg/ml inhibited the growth of many bacteria (7). Gibbs (5) has reviewed the literature which supports the hypothesis that oleoresin is important in the resistance of certain conifers to *F. annosus*. Data (5) show that the ability of a pine to mobilize resin largely determines its resistance to *F. annosus* and perhaps to many other diseases, although the mechanisms of resistance are not known. Resin accumulation was shown to act as a barrier to infection of white spruce roots by four heart rot fungi, but not by two others (22). *F. annosus* penetrated resin-impregnated xylem very slowly (2), but an inverse correlation between resin exudation and subsequent infection has also been reported (10). In addition, when oleoresin was bioassayed under conditions which allowed the volatile materials to escape, the resin acids were not toxic to either *F. annosus* (2) or to *Amylostereum* (3). Resins may act as a nontoxic water-proofing layer which prevents penetration of the wood by the fungus (19). Red pine wood collected from behind fire scars contained 35% resin, and decayed at

TABLE 4. Weight loss of cottonwood blocks impregnated with dehydroabietic acid or with a mixture of resin acids and exposed to *Coriolus versicolor* or to *Poria monticola* for 4 weeks at 27 C

Treatment	Concentration of impregnating solution (%)	Retention (%)	Weight loss[a] (% dry wt)	
			C. versicolor	*P. monticola*
None			18.8	23.9
Acetone alone			17.8	23.5
	1.5	1.5	18.0	25.0
Dehydroabietic	12	14.7	10.6**[b]	18.8*
acid	24	26.8	5.1**	12.4**
	38	37.2	1.6**	11.6**
Resin-acid	1.3	1.7	15.1	23.3
mixture	18	18.0	7.4**	16.1**
	27	25.2	6.0**	13.2**
	38	35.6	6.1**	12.4**

[a]Each value is the average of five blocks.
[b]* = differs significantly from the mean for acetone alone at $P = 0.05$, **, at $P = 0.01$

about the same rate as did wood from which resins had been extracted, when exposed to *Lentinus lepideus* (provided sufficient moisture was present in both samples) (19). The fact that fire scars on red pine are generally poor infection courts for decay fungi was attributed to the water-proofing nature of resins, rather than to their toxicity.

Different conclusions may have been reached on the role of resin acids as a protective agent, because of differences in techniques used to assay the effect of these complex materials as well as to differences in interpretation of the results. For example, our data (Table 4) show that the weight loss of blocks impregnated with acetone alone and then exposed to *P. monticola* for 4 weeks was 23.5%, whereas blocks impregnated with a 38% solution of resin acids lost about 12% of their weight. This latter figure is based on the assumption that the fungus is utilizing both the wood and the impregnated resin acids at the same rate. However, if in the resin-impregnated blocks the fungus did not metabolize any of the resin acids, then the rate of decay should be expressed on an extractive-free basis, since all the observed weight loss was caused by the utilization of wood by the fungus. If the weight loss values for blocks exposed to *P. monticola* are calculated on an extractive-free basis, they increase to 22-23%, almost identical with the control value. This strongly suggests that the apparent increase in decay resistance to *P. monticola* may be due to inability of the fungus to metabolize resin acids. However, the reduction in weight loss when the impregnated blocks were exposed to *C. versicolor* (Table 4) was so large that it cannot be solely attributed to inability of this fungus to metabolize resin acids. The results must reflect, in part at least, a slower rate of wood destruction.

The data on whether or not decay fungi are resinolytic are also somewhat conflicting. *Fomes pinicola* can utilize levopimaric acid as a sole source of carbon (18), and there is indirect evidence that *F. annosus* can metabolize the resin acids in pine wood (15). In addition, resin acids stimulated the growth and production of *Armillara mellea* rhizomorphs, and hence they may play a role in the colonization of roots by this fungus (14). However, spruce oleoresin at a concentration of 0.5% in malt agar inhibited mycelial growth of *F. annosus* by 50%; in a similar test, abietic acid at 0.25% inhibited mycelial growth approximately 60% (16).

Results of a previous study, where analyses were made before the labile acids could be oxidized or isomerized, indicated that the principal cortical resin acids in white spruce seedlings were levopimaric/palustric, and isopimaric (21). The large amount of dehydroabietic acid in samples from trees A and B probably resulted from the treatment (primarily heating) prior to analysis, as conjugated dienoic resin acids (i.e., levopimaric/palustric) isomerize rapidly under these conditions with a resulting increase in the quantity of dehydroabietic acid (8,9). Over a period of time, a mixture of resin acids exposed to normal atmospheric conditions would be expected to undergo similar modifications.

In conclusion, wounding of *P. glauca* resulted in a resin-soaked zone in the sapwood which was resistant to decay by *P. monticola* and *C. versicolor*. The resin-soaked tissue had an acidic pH value, and normal lignan content. The high resin content in this tissue was the most probable cause of increased decay resistance.

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